

Occasional Papers on Mollusks

Published by
THE DEPARTMENT OF MOLLUSKS
Museum of Comparative Zoölogy, Harvard University
Cambridge, Massachusetts

Volume 5

1 August 1997

Number 73

THE EFFECT OF BREEDING PERIOD ON THE BIOGEOGRAPHY OF FRESHWATER MUSSELS (BIVALVIA: UNIONOIDEA) IN THE MINNESOTA REGION OF NORTH AMERICA

Daniel L. Graf¹

ABSTRACT. The freshwaters of Minnesota are biogeographically significant as they form the headwaters of the Great Lakes, Hudson Bay, and Mississippi River basins. The 46 species of freshwater pearly mussels (Bivalvia: Unionoidea) that inhabit Minnesota can be divided into two general breeding types based on the length of their brooding period: *tachytictic*, or short-term brooding, and *bradytictic* long-term brooders. During the late glacial northern re-expansion of the Unionoidea into Minnesota, the completion of the life-cycle of short-term breeding mussels was inhibited by the harsh meltwater conditions. This led to the preferential establishment of certain bradytictic Mississippi species in ice-contact, meltwater environments. This tendency is reflected in the distribution of the Unionoidea of Minnesota; only nine species were able to freely disperse throughout the region until Recent climatic improvement. All other species invaded postglacially.

¹ Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.
E-mail: dgraf@oeb.harvard.edu.

INTRODUCTION

The effect of brooding period duration on the zoogeography of freshwater pearly mussels (Bivalvia: Unionoidea) in the Minnesota Region of North America is here reviewed. The generalized life cycle of freshwater mussels is well documented (for summaries, see Coker *et al.*, 1921; Kat, 1984). Equally well known is the variation that occurs at different stages in their life history (*i.e.*, glochidial morphology, marsupial anatomy, length of larval brooding period, *etc.*). However, the implications of these different reproductive strategies on the biology of mussels have been paid little attention.

As noted by Sterki (1895, 1898, 1903), freshwater mussels are divisible into two general breeding types; he referred to them as winter- and summer-breeders. However, as suggested by Lefevre and Curtis (1912), these breeding types are more accurately defined by the length of their brooding period rather than its seasonality.

Tachytictic (short-term/summer breeding) mussels spawn (*i.e.*, release their gametes) in the spring and expel their glochidia by the end of summer, brooding them in ctenidial marsupia only until mature. Mussels exhibiting *bradytictia*²

² The terms *tachytictic* and *bradytictic* were coined by Ortmann (1911) to describe short- and long-term breeding mussels, respectively. Davis and Fuller (1981) suggested the suffix *-ixis* for the noun formation (*e.g.*, *tachytixis*). However, this formation is considered improper (Zeph Stewart, Andrew W. Mellon Professor, *Emeritus*, of the Humanities, Harvard University, letter to K.J. Boss, 18 March, 1996). Since this convention is not in wide use, the forms *tachytictia* and *bradytictia* are herein utilized as nouns, as suggested by Professor Stewart.

(long-term/winter breeders) spawn during the late summer and retain their mature glochidia until the following spring (Lefevre and Curtis, 1910, 1912; Ortmann, 1909, 1911). *Bradytictia* is the norm in the anodontine and lampsiline clades, and correlated with their mode of parentage is the modification of their marsupia to accommodate long-term brooding (Sterki, 1903; Ortmann, 1911; Lefevre and Curtis, 1912). Tachytictic taxa of the Amblemini and Pleurobemini [*sensu* Davis and Fuller (1981) and Lydeard *et al.*, 1996)] are generally tetragenous (with exceptions, *e.g.*, *Pleurobema*) and without ctenidial specialization.

The Minnesota Region of North America is biogeographically significant, being composed of the headwaters of the three major drainage basins east of the Rocky Mountains: Hudson Bay, Great Lakes, and Mississippi (Graf, 1997a). As a political entity rather than a faunal province, the arbitrary yet well-known state boundaries limit the scope of this study; concepts applied to a particular basin within the Region, however, apply outside as well.

DISTRIBUTION OF BREEDING TYPES IN THE MINNESOTA REGION

Table 1 lists the 46 species of freshwater pearly mussels that inhabit Minnesota, including their distributions and breeding types. The breeding periods of mussel species in the Region generally conform to those predicted by their taxonomic affinities (Sterki, 1895, 1898, 1903; Frierson, 1904; Conner, 1907, 1909; Ortmann, 1909, 1911, 1919; Lefevre and Curtis, 1910, 1912; Surber, 1912, 1913; Howard, 1914, 1915; Utterback, 1916; Coker *et al.*, 1921; Baker, 1928; Clarke and Berg, 1959; Yokley, 1972; Clarke, 1981, 1985; Gordon and Smith, 1990; Haggerty *et al.*, 1992; Woody and Holland-Bartels, 1993; see additional references in Watters,

1994). Five noteworthy exceptions are *Cumberlandia monodonta*, *Megalonaias nervosa*, *Utterbackia imbecillis*, *Simpsonias ambigua*, and *Obliquaria reflexa*.

Cumberlandia monodonta (i.e., the Margaritiferidae, in general) has been described by some as being bradytictic (e.g., Heard and Guckert, 1970) and tachytictic by others (Sterki, 1903; Conner, 1909; Ortmann, 1911). The latter seems more correct based on the absence of marsupial adaptations for long-term glochidial brooding, such as those of the Anodontinae and Lampsilini (Davis and Fuller, 1981). However, the shoe-horning of margaritiferids into unionid categories may make this a moot point. Both Howard (1915) and Gordon and Smith (1990) suggested that *C. monodonta* may produce two broods per year. Thus, *Cumberlandia* may be neither in terms of unionid breeding types (or both!).

The placement of *Megalonaias nervosa* among the Amblemini suggests that it is a short-term breeder; however, its period of gravidity led early taxonomists to hesitantly describe it as bradytictic (Surber, 1912; Utterback, 1916; Lydeard *et al.*, 1996). Frierson (1904) reported that Louisiana specimens were gravid from October to January. Similar results were reported by Howard (1914, 1915) and Woody and Holland-Bartels (1993) further north; *M. nervosa* was found gravid from late August to early November. Lefevre and Curtis (1912) discovered gravid individuals in late May, but Howard (1914) confirmed that this condition occurred in only 2% of the *Megalonaias* he found. Thus, although the chronology of the breeding period of *M. nervosa* is anomalous, the length of its brooding period supports its position among the tachytictic (Lefevre and Curtis, 1910, 1912; Howard, 1914, 1915).

It has been demonstrated that *Utterbackia imbecillis* is bradytictic (like other *Anodonta*) and undergoes

Table 1. The Distribution of the Unionoidea in the Minnesota Region and their Breeding Types.

LMRS = Lower Mississippi River System (Mississippi River and tributaries below St. Anthony Falls); UMRS = Upper Mississippi River System (above St. Anthony Falls); RRS = Red River System; LWS = Lake of the Woods System; LSS = Lake Superior System. X = presence in a particular basin; B = bradytictic; T = tachytictic; † = exception (see text).

Species	breeding					
	type	LMRS	UMRS	RRS	LWS	LSS
Upper Mississippi River Fauna:						
<i>Anodontoides ferussacianus</i> (Lea)	B	X	X	X	X	X
<i>Lampsilis cardium</i> Rafinesque	B	X	X	X	X	X
<i>Lampsilis siliquoidea</i> (Barnes)	B	X	X	X	X	X
<i>Lasmigona complanata</i> (Barnes)	B	X	X	X	X	X
<i>Lasmigona compressa</i> (Lea)	B	X	X	X	X	X
<i>Ligumia recta</i> (Lamarck)	B	X	X	X	X	X
<i>Pyganodon grandis</i> (Say)	B	X	X	X	X	X
<i>Strophitus undulatus</i> (Say)	B	X	X	X	X	
<i>Utterbackia imbecillis</i> (Say)	B [†]	X	X			X
Red River of the North Fauna:						
<i>Lasmigona costata</i> (Rafinesque)	B	X		X		
<i>Potamilus alatus</i> (Say)	B	X		X		
<i>Amblema plicata</i> (Say)	T	X		X		
<i>Fusconaia flava</i> (Rafinesque)	T	X		X		
<i>Quadrula quadrula</i> (Rafinesque)	T	X		X		
Lake Superior Fauna:						
<i>Elliptio complanata</i> (Lightfoot)	T				X	
Lower Mississippi River Fauna³:						
<i>Cumberlandia monodonta</i> (Say)	? [†]	X				
<i>Megaloniais nervosa</i> (Rafinesque)	T [†]	X				
<i>Obliquaria reflexa</i> Rafinesque	T [†]	X				
<i>Simpsoniais ambigua</i> (Say)	B [†]	X				

³ The remaining mussels of the Lower Mississippi River Fauna are similarly distributed and either bradytictic [*Actinonaias ligamentina* (Lamarck); *Alasmidonta marginata* Say; *Anodonta suborbiculata* Say; *Arcidens confragosus* (Say); *Ellipsaria lineolata* (Rafinesque); *Epioblasma triquetra* (Rafinesque); *Lampsilis higginsii* (Lea); *Lampsilis teres* (Rafinesque); *Leptodea fragilis* (Rafinesque); *Obovaria olivaria* (Rafinesque); *Potamilus capax* (Green); *Potamilus ohioensis* (Rafinesque); *Toxolasma parvus* (Barnes); *Truncilla donaciformis* (Lea); *Truncilla truncata* (Rafinesque); *Venustaconcha ellipsiformis* (Conrad)] or exhibit tachytictia [*Cyclonaias tuberculata* (Rafinesque); *Elliptio crassidens* (Lamarck); *Elliptio dilatata* (Rafinesque); *Fusconaia ebena* (Rafinesque); *Plethobasus cyphus* (Rafinesque); *Pleurobema coccineum* (Conrad); *Quadrula fragosa* (Conrad); *Quadrula metanевра* (Rafinesque); *Quadrula nodulata* (Rafinesque); *Quadrula pustulosa* (Rafinesque); *Tritogonia verrucosa* (Rafinesque)].

metamorphosis on a fish host (like the rest of the Unionoidea) (Ortmann, 1909, 1919; Utterback, 1916; Clarke and Berg, 1959). It has also been reported that metamorphosis without parasitism can occur within the marsupia of this species (Howard, 1915; Howard and Anson, 1923; Allen, 1924) and that the breeding period lasts only a few weeks and may occur repeatedly throughout the year (Allen, 1924). As far as northern populations are concerned, however, Heard (1975) reported that bradytictia is exclusively encountered.

The data on *Simpsonaias ambigua* are so meager that direct evidence of its breeding times and brooding period are, for the most part, unavailable. Howard (1915; repeated in Clarke, 1985) collected *Necturus* (the mud puppy) infected with the glochidia of this species in October. These glochidia took the entire winter for metamorphosis in Howard's lab. The only observational data available suggests that *S. ambigua* releases its glochidia in the fall; its evolutionary relationships suggest bradytictia.

The decidedly lampsiline modifications of the marsupium of *Obliquaria reflexa* suggest that it might be placed among the long-term brooders (Ortmann, 1911; Utterback, 1916; Lydeard *et al.*, 1996). However, it has only been reported gravid from May or June to August (Lefevre and Curtis, 1910; Surber, 1912; Utterback, 1916; Ortmann, 1919) and is thus considered tachytictic.

DISCUSSION

The Minnesota Region is composed of five drainage systems (Figure 1). The Red River and Lake of the Woods systems are confluent at Lake Winnipeg, but their differing mussel communities warrant their division (Graf, 1997a). The Upper and Lower Mississippi River systems are separated by the Falls of St. Anthony at Minneapolis, a barrier

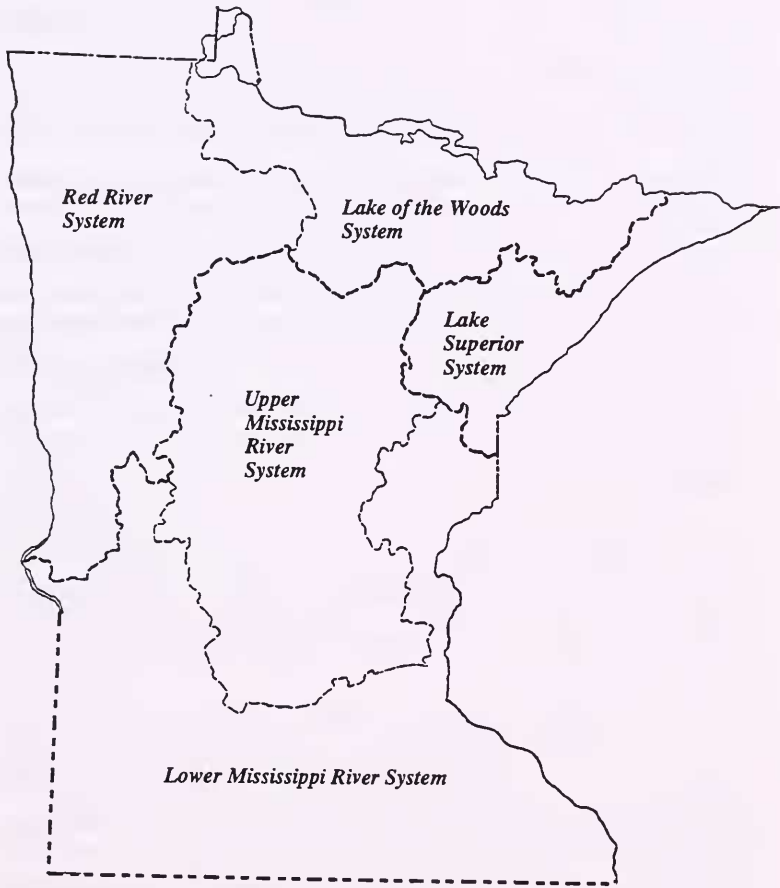


Figure 1. The drainage systems of the Minnesota Region (redrawn from Graf, 1997a)

to mussel distribution via their host fishes (Underhill, 1989; Graf, 1997b). All Unionoidea occurring in Minnesota except *Elliptio complanata* (see below) migrated into the Region from unglaciated refugia in the Mississippi below the maximum extent of Pleistocene glaciation (Johnson, 1980).

As discussed by Graf (1997b), the earliest invading mussel community arrived in the Region sometime after 14,000 years before present (bp) when central Minnesota became ice-free and before 11,000 bp, the latest date of formation for St. Anthony Falls. These unionoideans correspond to the Upper Mississippi River Fauna (UMRF) of Graf (1997a) (Table 1). The remaining mussel species migrated into the Region post-glacially; this includes those five species occurring in addition to the UMRF in the Red River system: they entered that basin after 9500 bp either via high water through Lakes Big Stone and Traverse or, more likely, stream capture in the Otter Tail River watershed (Graf, 1997b).

As Table 1 shows, the UMRF is completely bradyctic. Thus, all of the mussel species present in the Region for at least 1500 years (i.e., from before 11,000 to 9500 bp) were long-term breeders that brooded their glochidia over the frigid winter months.

The observed dominance of bradyctic species in the earliest invading mussel fauna in the Minnesota Region has an analog in the northern Atlantic Slope drainage of eastern North America (Graf, 1996). Both there and in Minnesota, obliteration of the unionoidean community by Wisconsin glaciation was followed by repopulation from unglaciated refugia; subsequent development of a barrier then halted further mussel migration. In the case of the northern Atlantic Slope, it was the rise in sea level as continental ice melted (Johnson, 1970) and the creation of fall lines (D. Smith, pers. comm.) that curtailed further dispersal; in the Minnesota

Region it was the formation of St. Anthony Falls and the drop in water level associated with glacial retreat from the Region (Graf, 1997b). The mussel fauna of the northern Atlantic Slope is mostly bradytictic (87%; Graf, 1996).

With the retreat of glacial ice from the Minnesota Region, aquatic connections existed (Clayton and Moran, 1982) that would have allowed the newly deglaciated area to be repopulated from unglaciated refugia (Underhill, 1989; Graf, 1997b). The conditions of these periglacial meltwater streams were probably more severe than in rivers of the Minnesota Region today, with near-freezing melt water and a greater silt load; newly deglaciated Minnesota was boreal spruce forest until perhaps 8000 bp (Barry, 1983). Such an environment is indicative of a cooler climate and a shortened growing season.

A shortened growing season would have inhibited the ontogeny of tachytictic mussels. The period prior to completion of metamorphosis is the time of greatest mortality (McMahon, 1991), and cold temperatures can slow metamorphosis from a few to hundreds of days (Howard and Anson, 1923). With a later spring and earlier fall, the summer breeding season would be shortened; tachytictic glochidial encystment and metamorphosis would have to begin while temperatures were declining. Glochidia released in the following spring, however, would have the entire growing season for their development.

Such conditions existed in the Minnesota Region and inhibited the establishment of tachytictic species. With the development of barriers to further dispersal, additional, possibly tachytictic mussel species, were no longer able to colonize the Region beyond the lower Mississippi drainage (the Mississippi River and its tributaries below St. Anthony Falls) subsequent to climatic improvement. This explanation is appropriate on the northern Atlantic Slope as well.

Relevant to this discussion is Hutchins' (1947) generalization regarding the breeding time of marine invertebrates. Animals that begin breeding in the fall do so because summer temperatures are too warm; those that begin in the spring do so because winter conditions are too harsh. The former, with regard to the Unionoidea, is bradytictia, the latter tachytictia. Coker *et al.* (1921) noted that generally the long-term breeders begin their annual reproduction on the falling temperatures of late summer, while spawning in tachytictic forms is initiated by rising spring temperatures. According to Hutchins (1947), animals that spawn as temperatures drop have a tendency to move in a pole-ward direction, while summer breeders do the opposite. This supports the selective dispersal of bradytictic freshwater mussels to northern, cooler waters from warmer southern refugia.

Both Sterki (1903) and Ortmann (1909) speculated about the phylogenetic significance of these differences in the larval brooding period. According to Ortmann (1919), who recognized the Pleurobemini and Amblemini (= "Unioninae") as the phylogenetically least derived unionid clade, tachytictia developed early in the Tertiary when the climate was more mild; long-term breeding evolved in response to the harsh glacial climate and shortened growing season of the late Tertiary and Quaternary. Conflicting with this interpretation is the opinion that bradytictia is ancestral in the Unionoidea (Heard and Guckert, 1970; Davis and Fuller, 1981). However, there can be little doubt of Sterki's (1903) conclusion that differences in brood period among the taxa are a reflection of the climatic regime of their ancestors.

CONCLUSIONS

The length of the brooding period can not be the only

factor that determined the chronology of northward range expansion of freshwater pearly mussels at the close of the Pleistocene. Regardless of a mussel's ability to survive and produce glochidia under periglacial conditions, its host must not only have been tolerant of the same environment (at least during the mussel's breeding period) but also have been present. The necessity of the combination of cold-tolerant mussel and host may explain the paucity of unionoideans that invaded Minnesota immediately following Wisconsin glaciation.

ACKNOWLEDGMENTS

I would like to thank R.I. Johnson and K.J. Boss for their many suggestions and comments toward the improvement of this study.

REFERENCES CITED

- Allen, E. 1924. The existence of a short reproductive cycle in *Anodonta imbecillis*. *Biological Bulletin* **46**: 88-94.
- Baker, F.C. 1928. The fresh water Mollusca of Wisconsin. Wisconsin Geological and Natural History Survey Bulletin **70**: 1-495, pls. 1-105.
- Barry, R.G. 1983. Late-Pleistocene climatology. pp. 390-407. [In] S.C. Porter (ed.). Volume I: The Late Pleistocene. [In] H.E. Wright, jr. (ed.). Late-Quaternary Environments of the United States.
- Clarke, A.H. 1981. The tribe Alasmidontini (Unionidae: Anodontinae), Part I: *Pegais*, *Alasmidonta*, and *Arcidens*. *Smithsonian Contributions to Zoology* (326): 1-101.
- Clarke, A.H. 1985. The tribe Alasmidontini (Unionidae: Anodontinae), Part II: *Lasmigona* and *Simpsonaias*. *Smithsonian Contributions to Zoology* (399): 1-75.

- Clarke, A.H., C.O. Berg. 1959. The freshwater mussels of central New York. Cornell University, Agriculture Experimental Station, Memoir (367): 1-79.
- Clayton, L., S.R. Moran. 1982. Chronology of Late Wisconsin glaciation in Middle North America. *Quaternary Science Reviews* **1**: 55-82.
- Coker, R.E., A.F. Shira, H.W. Clark, and A.D. Howard. 1921. Natural history and propagation of freshwater mussels. *Bulletin of the Bureau of Fisheries* **37**: 77-181. (Reprinted as Bureau of Fisheries Document No. 893.)
- Conner, C.H. 1907. The gravid period of unios. *Nautilus* **22**: 87-89.
- Conner, C.H. 1909. Supplementary notes on the breeding seasons of the Unionidæ. *Nautilus* **22**: 111-112.
- Davis, G.M., S.L.H. Fuller. 1981. Genetic relationships among Recent Unionacea (Bivalvia) of North America. *Malacologia* **20**: 217-253.
- Frierson, L.S. 1904. Observations on the genus *Quadrula*. *Nautilus* **17**: 111-112.
- Gordon, M.E., D.G. Smith. 1990. Autumnal reproduction in *Cumberlandia monodonta* (Unionoidea: Margaritifera). *Transactions of the American Microscopical Society* **109**: 407-411.
- Graf, D.L. 1996. The Brady Bunch: A preliminary look at the bradyticic Unionoidea and their taxonomic and geographic distribution in the Atlantic Slope region of North America. *NU-Biology, A Newsletter of Research Synopsis [sic] and Proposals at Northeastern University* **2**(2): 1-3.
- Graf, D.L. 1997a. Distribution of unionoid (Bivalvia) faunas in Minnesota, USA. *Nautilus* **110**: 45-54.
- Graf, D.L. 1997b. Northern redistribution of freshwater pearly mussels (Bivalvia: Unionoidea) during Wisconsin deglaciation in the southern Glacial Lake Agassiz region: a review. *American Midland Naturalist* **138**, in press.

- Haggerty, T.M., G.P. Patterson, L.C. Jones. 1992. Aspects of the reproductive biology of *Cyclonaias tuberculata* (Unionidae: Bivalvia). *Journal of Alabama Academy of Science* **63**: 56 [abstract].
- Heard, W.H. 1975. Sexuality and other aspects of reproduction in *Anodonta* (Pelecypoda: Unionidae). *Malacologia* **15**: 81-103.
- Heard, W.H., R.H. Guckert. 1970. A re-evaluation of the Recent Unionacea (Pelecypoda) of North America. *Malacologia* **10**: 333-355.
- Howard, A.D. 1914. Experiments in propagation of fresh-water mussels of the *Quadrula* group. Report of the Commissioner of Fisheries for the Fiscal Year 1913, Appendix 4: 1-52, 6 pls. (Reprinted as Bureau of Fisheries Document No. 801.)
- Howard, A.D. 1915. Some exceptional cases of breeding among Unionidae. *Nautilus* **29**: 4-11.
- Howard, A.D., B.J. Anson. 1923. Phases of parasitism of the Unionidae. *Journal of Parasitology* **9**: 68-82, pls. 7-8.
- Hutchins, L.W. 1947. The bases for temperature zonation in geographical distribution. *Ecological Monographs* **17**: 325-335.
- Johnson, R.I. 1970. The systematics and zoogeography of the Unionidae (Mollusca: Bivalvia) of the southern Atlantic Slope region. *Bulletin of the Museum of Comparative Zoology* **140**: 263-449.
- Johnson, R.I. 1980. Zoogeography of North American Unionacea (Mollusca: Bivalvia) north of maximum Pleistocene glaciations. *Bulletin of the Museum of Comparative Zoology* **149**: 77-189.
- Kat, P.W. 1984. Parasitism and the Unionacea (Bivalvia). *Biological Reviews* **59**: 189-207.
- Lefevre, G., W.C. Curtis. 1910. Experiments in the artificial propagation of fresh-water mussels. *Bulletin of the U.S. Bureau of Fisheries* **28**: 615-626. (Reprinted as Bureau of Fisheries Document No. 671.)
- Lefevre, G., W.C. Curtis. 1912. Studies on the reproduction and artificial propagation of fresh-water mussels. *Bulletin of the U.S.*

- Bureau of Fisheries 30: 105-201, pls. 6-17. (Reprinted in parts in Sterkiana, 1972-1976.)
- Lydeard, C., M. Mulvey, G.M. Davis. 1996. Molecular systematics and evolution of reproductive traits of North American freshwater unionacean mussels (Mollusca: Bivalvia) as inferred from 16S rRNA gene sequences. *Philosophical Transactions of the Royal Society of London B* 351: 1593-1603.
- McMahon, R.F. 1991. Mollusca: Bivalvia. pp. 315-399. [in] J.T. Thorp and A.P. Covich (eds.). *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press, New York.
- Ortmann, A.E. 1909. The breeding season of Unionidæ in Pennsylvania. *Nautilus* 22: 91-95, 99-03.
- Ortmann, A.E. 1911. Monograph of the naiades of Pennsylvania. I. Anatomical investigations. Part II. The system of North American najades. *Memoirs of the Carnegie Museum* 4: 279-347, pls. 86-89.
- Ortmann, A.E. 1919. Monograph of the naiades of Pennsylvania. III. Systematic account of the genera and species. *Memoirs of the Carnegie Museum* 8: 1-385.
- Sterki, V. 1895. Some notes on the genital organs of Unionidæ, with reference to systematics. *Nautilus* 9: 91-94.
- Sterki, V. 1898. Some observations on the genital organs of Unionidæ, with reference to classification. *Nautilus* 12: 18-21, 28-32.
- Sterki, V. 1903. Notes on the Unionidæ and their classification. *American Naturalist* 37: 103-113.
- Surber, T. 1912. Identification of the glochidia of freshwater mussels. Report of the Commissioner of Fisheries for the Fiscal Year 1912 and Special Papers: 1-10. (Reprinted as Bureau of Fisheries Document No. 771.)
- Surber, T. 1913. Notes on the natural hosts of fresh-water mussels. *Bulletin of the U.S. Bureau of Fisheries* 32: 101-115, pls. 29-31. (Reprinted as Bureau of Fisheries Document No. 778.)

- Underhill, J. 1989. The distribution of Minnesota fishes and Late Pleistocene glaciation. *Journal of the Minnesota Academy of Science* **55**: 32-37.
- Utterback, W.I. 1916. Breeding record of Missouri mussels. *Nautilus* **30**: 13-21.
- Watters, G.T. 1994. An Annotated Bibliography of the Reproduction and Propagation of the Unionoidea (Primarily of North America). Ohio Biological Survey Miscellaneous Contribution No. 1. 158 pp.
- Woody, C.A., L. Holland-Bartels. 1993. Reproductive characteristics of a population of the washboard mussel *Megalonaias nervosa* (Rafinesque 1820) in the upper Mississippi River. *Journal of Freshwater Ecology* **8**: 57-66.
- Yokley, P. 1972. Life history of *Pleurobema cordatum* (Rafinesque) (Bivalvia: Unionacea). *Malacologia* **11**: 351-364.